# Estimating Handling Mortality Due to Air Exposure: Development and Application of Thermal Models for the Bering Sea Snow Crab Fishery

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*Abstract.*—The fishery for snow crabs *Chionoecetes opilio* in Alaska occurs during the winter, and handling mortality may be high due to cold-air exposure. Heat budget models that include convection, evaporation, long-wave radiation, and solar radiation were developed for snow crabs. Model performance was evaluated by comparing observed and predicted temperatures of live crabs exposed to cold air. The model performed well, predicting temperatures of the body, legs, and eyes within 1.5°C. Legs and eyes cooled faster than the body and may be more susceptible to cold-air exposure. Weather variables were ranked in the following order of importance: (1) air temperature, (2) solar radiation, (3) wind speed, (4) humidity, and (5) cloud cover. Clear, cold, breezy nights are the most detrimental conditions for crabs. Hourly weather records from a site near the fishing grounds were used in conjunction with the thermal model to estimate cooling rates for crabs every hour during actual and hypothetical seasons. The probability of damage for various cooling rates was estimated based on previously published laboratory data. Discard handling damage rates were highly variable, ranging from 0% to 30% over 21 actual fishing seasons. Damage rates for hypothetical seasons that varied in length, start day, and daily fishing hours were calculated. Damage rates were reduced by delaying the start day (15 January) until 1 March as well as by limiting fishing time to daylight hours. Combining a later starting day with limited fishing hours resulted in 90% of the hypothetical seasons having damage rates of 10% or less. Generally, longer seasons had lower damage rates, especially when fishing hours were limited. Although developed for cold-weather Alaska fisheries, this approach can easily be adapted to other fisheries where handling mortality due to temperature changes during capture is a concern.

The capture of unwanted fish has been recognized as an important problem for many years (Jean 1962; Powles 1969; Brown and Caputi 1983; Pautzke 1997). Earlier concerns were centered on the catch of nontarget species, but in fisheries with size limits there can also be problems with catching individuals of the target species that are returned to the sea. The death of target and nontarget species bycatch returned to the sea, or discards, is termed handling mortality. Most of the focus to date has been on reducing the catch rate of discards, whereas relatively little effort has been applied to determining the fate of discards after they have been returned to the sea. Reducing handling mortality rates along with reducing the catch of unwanted individuals can be instrumental in ameliorating this problem.

When they are captured and brought to the surface, fish (used here to refer to both vertebrates and invertebrates) may experience many different kinds of stress. Fish may incur injuries from contact with fishing gear and other fish or may suffer from the effects of changing pressure. As fish are brought to the sea surface, they may be subjected to temperature changes while passing through the thermocline and when exposed to air (e.g., Richards et al. 1995; Davis et al. 2001; DiNardo et al. 2002; Warrenchuk and Shirley 2002a, 2002b). Depending upon the fishery, exposure to air can last from minutes to hours (Davis 2002). Other effects of capture include increased light levels and anoxia. Smaller fish are generally more susceptible to handling effects than are larger fish (Richards et al. 1995; Ross and Hokenson 1997).

Although some work is being done to assess the handling mortality of finfish, less has been done in this regard for shellfish fisheries. Because of the gear used and the biological properties of crabs, mortality due to interactions with the gear, transport through the water column, and handling on deck appears to be minimal (Zhou and Shirley 1995, 1996; MacIntosh et al. 1996), leaving exposure to air as the remaining substantial source of mortality. Anoxia does not appear to be im-

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portant, as many crustaceans can withstand pro-longed periods of air exposure as long as the tem-peratures are not extreme (McCleese 1964; Brown and Caputi 1983; Kruse et al. 1994; DiNardo et al. 2002). Most studies have considered the im-plications of exposure to air warmer than the water temperature (Denny 1993; Bell 1995; Helmuth 1998, 1999; Davis 2002; DiNardo et al. 2002). In winter fisheries at high latitudes, deleterious ef-fects may result from exposure to cold air (Carls and O'Clair 1990, 1995; Warrenchuk and Shirley 2002a, 2002b). Many studies of trawling bycatch have correlated mortality to time on deck, air tem-perature, water temperature, catch size, and body size (Jean 1962; Powles 1969; Richards et al. 1995; Ross and Hokenson 1997), suggesting that body temperature is an important variable in de-termining handling mortality.

Air temperature is the most common, and often the only, environmental condition considered when evaluating temperature stress due to air ex-posure (Carls and O'Clair 1990, 1995; Olla et al. 1997, 1998; Davis and Olla 2001, 2002; Davis et al. 2001). There are, however, many other envi-ronmental conditions that can influence body tem-perature or the rate of body temperature change (Denny 1993; Campbell and Norman 1998). The most commonly known of these is the added effect of wind on cooling rates. This is often referred to as wind chill (Court 1948) but is more correctly termed convection. Warrenchuk and Shirley (2002a, 2002b) applied the idea of wind chill to crab cooling in the laboratory and found that the exposure time needed to cause mortality in crabs exposed to wind was substantially lower than that of crabs exposed to cold, still air (Carls and O'Clair 1990, 1995). Wind chill, however, is an imprecise measure of the complex process of heat loss and should be used only as a clothing guide for humans in cold weather (Bluestein 1998; Blue-stein and Zecher 1999). More thorough studies of heat exchange have been performed for a variety of organisms to predict body temperatures, met-abolic rates, and activity schedules (Porter et al. 1973; Mitchell 1976; Muth 1977, 1980; Porter and McClure 1984; Denny 1993; Bell 1995). This study uses these techniques to investigate the heat transfer of crabs exposed to cold air as an example of a fishery with handling mortality caused by tem-perature changes due to air exposure.

Studies investigating the temperature changes of organisms usually focus on the core body tem-perature. While this may be a good indicator of future mortality, it overlooks the effects of tem-perature change on extremities. In some taxa, such as mussels (Helmuth 1998, 1999), this focus on core body temperature is justified. In taxa that have legs, eyes, or other sensory structures set off from the body, such as crabs and some finfish, a focus on core body temperature will miss some poten-tially critical effects of air exposure. For example, individuals that incur damage to sensory structures during handling may survive well in captivity but in the wild may be eaten or may fail to obtain enough food, leading to delayed mortality. Know-ing how appendages respond to air exposure may aid in our overall understanding of handling mor-tality.

In Alaska, fisheries for Tanner crabs *Chionoe-cetes bairdi*, snow crabs *C. opilio*, red king crabs *Paralithodes camtschaticus*, blue king crabs *P. platypus*, and golden king crabs *Lithodes aequis-pinus* generally occur between November and March, and handling mortality may be substantial. Conditions during Alaskan crab fisheries can be severe: air temperatures can be less than −20°C, and winds can exceed 30 m/s. Even though crab pots are designed to allow small crabs to escape, sublegal and female crabs can constitute 32–79% of the catch (Kruse et al. 2000). Although some attempts have been made to design crab pots that limit the catch of unwanted crabs (Zhou and Shir-ley 1997), they have met with limited success dur-ing test fisheries. A few studies investigating the effect of cold-air exposure on Alaskan crabs sug-gest that deleterious effects can occur under nor-mal climatic conditions and within the time frame of sorting procedures (Carls and O'Clair 1990, 1995; Warrenchuk and Shirley 2002a, 2002b), but the actual mortality due to handling crabs in cold weather is currently unknown. Several proposals have been considered by the Alaska Board of Fish-eries that would change the season start date of the snow crab fishery in an effort to reduce han-dling mortality, but there has been little infor-mation to evaluate these proposals (Pengilly et al. 2001).

This paper develops a thermal model of heat exchange mechanisms that occur when Tanner and snow crabs are exposed to air during winter fish-eries. I used the model to address a number of fishery specific problems. By combining the model with historic weather data, crab micrometeorology, and crab damage rates determined from laboratory studies, I estimated the handling damage rates of past seasons. I also used hypothetical fishing sea-sons to determine the potential effects of delaying

the season start day, adjusting season length, and limiting fishing hours on handling damage rates.

## Methods

*Model development.*—Previous modelers have generally used the same basic techniques based upon the physics of heat exchange to determine the heat budget for various organisms and objects (Porter et al. 1973; Tracy 1976; Muth 1977; Helmuth 1998). These techniques identify mechanisms of heat exchange between the object of interest and the surrounding environment. There are five basic mechanisms of heat exchange: long-wave radiation, solar (short-wave) radiation, convection, evaporation, and conduction. The total heat transfer, expressed in watts, for the object is simply the sum of these five mechanisms. Temperature change can be calculated from heat transfer if the mass and specific heat of the object is known. This paper uses many of the same techniques developed by other researchers to investigate overheating of organisms, especially those detailed by Helmuth (1998), but here the techniques are adapted to investigate organism cooling.

*Long-wave radiation.*—Traditionally, the infrared radiation term has been divided between the sky and surrounding radiation because the sky emissivity varies, whereas the emissivity of most surrounding objects remains fairly constant. Emissivity for virtually all biological materials and most other materials is between 0.95 and 1.00 (Campbell and Norman 1998); for simplicity, I used a value of 1.00. The emissivity of the sky varies between 0.68 (clear skies) and 0.95 (cloudy skies), and can be readily estimated based on the air temperature and the percentage of sky that is clouded (Campbell and Norman 1998). From the equations given in Helmuth (1998) and the emissivities given above, the total heat transfer due to long-wave radiation ($Q_{rad}$) with the surroundings and sky is calculated as

$$Q_{rad,surr} = A_{rad,surr}\sigma(T_b^4 - T_{surr}^4) \quad \text{and}$$

$$Q_{rad,sky} = A_{rad,sky}\sigma(T_b^4 - \varepsilon_{sky}T_a^4),$$

where $A_{rad,surr}$ and $A_{rad,sky}$ are the surface areas for radiative exchange with the surroundings and sky; $T_b$, $T_a$, and $T_{surr}$ are the temperatures of the organism, air, and surroundings; $\varepsilon_{sky}$ is the emissivity of the sky; and $\sigma$ is the Stefan–Boltzman constant ($5.67 \times 10^{-8}$ W·m$^{-2}$·°K$^{-4}$). The surface areas for radiation to the sky and surroundings were estimated to be half the total surface area of the body or leg.

*Short-wave radiation.*—On average, the heat input of solar energy will be minimal in Alaskan winter fisheries because daylight hours are short and the sun's angle is low. There may, however, be times when this component of the heat budget is important, and it is the major source of heat input to many other organisms (Porter et al. 1973; Walsberg 1992; Helmuth 1998, 1999). The heat input from solar radiation ($Q_{sol}$) is relatively simple to estimate and depends upon the solar flux ($S$), the absorbtivity of crabs ($\alpha$), and the surface area available to solar radiation ($A_{sol}$), that is,

$$Q_{sol} = A_{sol}\alpha S.$$

The absorbtivity of crabs was estimated to be about 0.6, which is an average value for biological materials (Campbell and Norman 1998) and slightly lower than the value used by Helmuth (1998) for mussels. Solar radiation in the Bering Sea can have a large reflected component, so the crab area exposed to solar radiation was assumed to be 0.75 of the total surface area. Because of the diffuse nature of solar radiation in the Bering Sea, all measurements and estimates were taken as total horizontal radiation, including both direct and reflected components.

*Convection.*—The movement of air around a crab can dramatically increase the rate of heat loss to the surrounding air. The heat exchange due to convection ($Q_{conv}$) is governed by the temperature differential between the crab and air, the surface area of the crab ($A$), and the heat transfer coefficient ($h_c$), which incorporates properties of the surrounding fluid, flow patterns around the crab, and characteristics of the crab. The equation is as follows:

$$Q_{conv} = h_c A(T_b - T_a).$$

Although $h_c$ is known for many common shapes and these $h_c$ values have been successfully used to predict body temperatures of a variety of organisms (Porter and Gates 1969; Bakken 1992), a more accurate method is to determine $h_c$ empirically (O'Connor and Spotila 1992; Helmuth 1998), especially for organisms with complex shapes. Because $h_c$ was used to estimate the mass transfer coefficient for evaporative heat loss, I determined $h_c$ empirically.

To determine $h_c$, I eliminated all heat transfer pathways except convection and radiation. Replicas of crabs were constructed by using urethane molds and casting crabs in epoxy resin (see Morphometrics section below). Crab replicas were
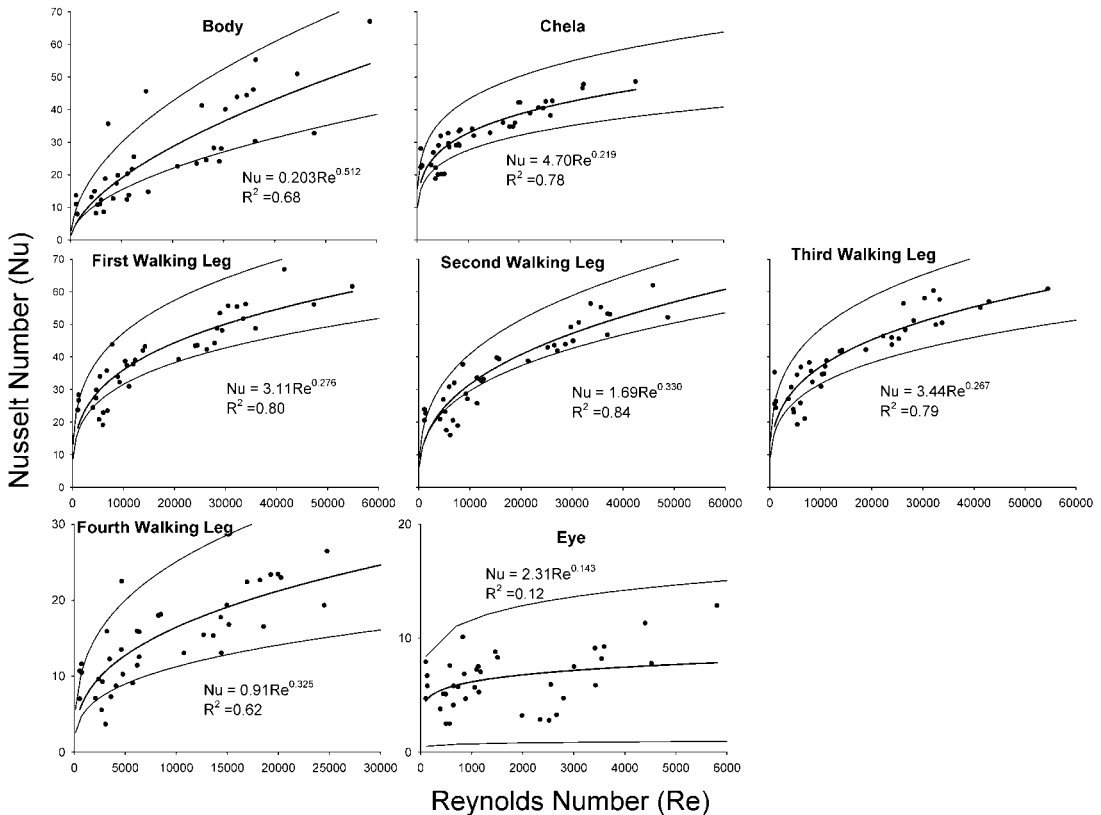
FIGURE 1.—The relationship between the Nusselt number and Reynolds number for snow crab bodies, legs, and eyes. The thick lines are the best-fit lines determined by nonlinear regression (SigmaPlot 1998). The thinner upper and lower lines were determined by the methods described in the text and represent the bounds used in other analyses.

heated to about 20–30°C above ambient temperature and were placed in a wind tunnel with turbulent flow. Crab replicas were exposed to wind and allowed to cool to within 2–6°C of ambient temperature. The temperature of each crab replica was monitored with thermocouples inserted into the center of the body, the center of the merus of all right-side legs, and the eye; temperature data were downloaded at a rate of 1.00–1.25 Hz with a data acquisition device (Omega Model OMB-DAQ-56) connected to a laptop computer. The $h_c$ was calculated from the resultant cooling curves by use of the methods outlined by Helmuth (1998).

The flow patterns and speed of the fluid around an animal can be described with the Reynolds number (Re); a similar, dimensionless number, the Nusselt number (Nu), is the heat-based analog of Re. The Nusselt number is typically presented as a power function of Re (Nu–Re plots) so that Nu can be estimated from Re. Because $h_c$ is used to calculate Nu, estimates of Nu can be used to estimate $h_c$. In this study, Nu–Re plots were generated for the bodies, legs, and eyes of crabs that were oriented with the anterior surface facing into the wind (Figure 1). Crab sizes varied from 83 to 103 mm (carapace width [CW]) and wind speed varied from 0.2 to 8.6 m/s, yielding a total Re range of about 1,000 to almost 60,000.

*Evaporative cooling.*—Heat loss due to the evaporation of water can be large. Crabs just pulled from the ocean will be covered in water, and it was assumed that they would not dry out during the maximum exposure time of 10–15 min. The total heat transfer due to evaporation ($Q_{evap}$) is simply the amount of water that evaporates times the latent heat of vaporization ($\lambda$). The rate of water evaporation is determined by the surface area of the organism, the difference in water vapor concentrations of the body surface ($C_b$) and the ambient air ($C_a$), and the mass transfer coefficient ($h_m$), as follows:

$$Q_{\text{evap}} = h_m A(C_b - C_a)\lambda.$$

The mass transfer coefficient is similar to $h_c$, and they can be interchanged for objects in air by using the Lewis Rule (O'Connor and Spotila 1992). The vapor concentration at the body surface was assumed to be equal to the saturation concentration of water in air at the temperature of the body. The water concentration in air was determined from the relative humidity and the air temperature.

*Conduction.*—Conduction of heat between the crab and the surfaces it comes in contact with was ignored. While the crabs are suspended in the crab pot, there will be little surface area over which conduction can occur, mostly consisting of the nylon mesh making up the bulk of the structure of the crab pot. Undoubtedly, crabs will contact the surface of the sorting table, but this was ignored for two reasons. First, the area of contact will be minimal due to the complex shape and topography of the crabs. Second, the long-wave radiation term for the surrounding surface yields roughly the same result as a conduction term would, and any area that is actually touching the table surface would need to be subtracted from the area available for long-wave radiation. Thus, the small amount of area that actually contacts the table is assumed to transfer heat at the same rate as those areas that are close to the table but not touching it.

*Morphometrics.*—Snow and Tanner crabs are morphologically complex, consisting of a central body with 10 relatively large legs. Because of the various spines and irregularities, surface areas of crabs are too complex to be treated as simple shapes. Surface areas were determined from crab replicas made for the determination of $h_c$. Crab replicas were made with commercially available molding and casting materials (Synair Por-A-Mold and Por-A-Kast). The legs of real crabs were removed prior to casting, and crab casts consisted of a body and 10 separate legs.

Before assembling the crab replicas, all crab parts were measured in a manner similar to that used for the real crabs described below. Surface area was determined for each part by dipping the part in dishwashing liquid, letting the liquid drip for 2 min, and weighing before and after wetting. Surface area was obtained by determining the weight of the liquid (wetted weight minus the weight of the dry part) and comparing this value to the weight gain of a cylinder (109.7 mm long × 24.4 mm in diameter) made with the same tech-

TABLE 1.—The results of regression analyses predicting the characteristic length (CL), surface area (SA), and mass from the carapace width of snow crabs ($n = 52$). All analyses were performed on $\log_e$ transformed data except for those marked with an asterisk, where raw data were used. Leg 1 is the chela; legs 2–5 are the walking legs.

| Part | y-intercept | Slope | $R^2$ | $F$ |
|---|---|---|---|---|
| Body SA | 0.413 | 2.033 | 0.993 | 7,548.06 |
| Body mass | −7.944 | 2.896 | 0.981 | 2,646.90 |
| Eye CL | −0.818 | 0.664 | 0.889 | 401.66 |
| Eye SA | −0.937 | 1.262 | 0.895 | 426.09 |
| Eye mass | −9.870 | 1.859 | 0.881 | 371.03 |
| Leg 1 CL* | −21.454 | 0.855 | 0.872 | 340.90 |
| Leg 1 SA* | −11,828.41 | 206.393 | 0.898 | 439.43 |
| Leg 1 mass* | −82.021 | 1.200 | 0.893 | 415.31 |
| Leg 2 CL | −0.559 | 1.106 | 0.909 | 499.72 |
| Leg 2 SA | −1.567 | 2.258 | 0.964 | 1,327.99 |
| Leg 2 mass | −11.525 | 3.191 | 0.964 | 1,346.96 |
| Leg 3 CL | −0.432 | 1.075 | 0.899 | 445.99 |
| Leg 3 SA | −1.102 | 2.137 | 0.961 | 1,234.93 |
| Leg 3 mass | −11.100 | 3.067 | 0.957 | 1,104.35 |
| Leg 4 CL | −0.278 | 1.013 | 0.896 | 430.29 |
| Leg 4 SA | −1.289 | 2.117 | 0.965 | 1,367.10 |
| Leg 4 mass | −11.020 | 2.987 | 0.958 | 1,140.98 |
| Leg 5 CL | −0.627 | 0.993 | 0.890 | 404.16 |
| Leg 5 SA | −1.505 | 2.038 | 0.966 | 1,424.11 |
| Leg 5 mass | −11.728 | 2.944 | 0.948 | 903.94 |

nique used to make the crab replicas. Based on the two crab replicas that were measured for surface area, I also calculated the surface areas under the assumption that the crabs were composed of relatively simple shapes. The ratio of measured surface area to calculated surface area yielded a correction factor that could be multiplied by calculated values for any crab to yield an estimate of surface area.

To determine the relationship between CW and mass, surface area, and characteristic length of all crab parts, I measured 52 crabs for a number of morphological characteristics. The carapace and all sections of each leg (except the basi-ischium, which was included with the merus) were measured for width, depth, and length. The maximum width and depth of each leg were measured, but the total length of the leg was approximated by adding all of the leg section lengths. These measurements were then used to calculate surface area by assuming that the body and legs were a series of ovoid spheres, cylinders, and cones and multiplying by the correction factors obtained from the replicas. All legs were removed from each crab, and the body and right-side legs were weighed. Carapace width was then used to predict the mass, surface area, and characteristic length of the body, each leg, and the eye (Table 1).

*Simple-shape model.*—I compared the realistic model to a model based upon simple geometric shapes that took days rather than months to develop. The simple-shape model eliminated the need to empirically estimate $h_c$ and estimate surface areas, which comprised the major portion of the work in developing the realistic model.

The simple-shape model consisted of a sphere representing the body and cylinders for the legs. The size of the sphere was determined from the CW of the crab being modeled. Carapace width was first converted to body mass by use of the relationship described in the Morphometrics section, and then the diameter of the sphere was calculated so that the mass of the sphere would equal the mass of the body assuming a density of 1,150 kg/m³. Similarly, the masses of the legs were calculated from the morphometric relationship, and the diameter of the cylinder was then determined assuming the same density and a cylinder length of twice the CW for all legs except the fourth walking leg, which was considered to be 1.5 times the CW. Heat transfer coefficients were obtained from the literature (Mitchell 1976). All other terms in the simple-shape model were the same as for the realistic model. This model was then used to predict body temperature during the field trials.

*Field tests of the model.*—To test the accuracy of the model, I exposed live crabs to air and recorded body temperature, leg temperature, and microclimate data in Juneau, Alaska. I attempted to test the model in a wide variety of environmental conditions to understand the generality of the model. Most of the field trials were conducted with snow crabs between 9 January and 24 February 2003 and consisted of monitoring the body, leg, and eye temperatures of the crabs with thermocouples while simultaneously recording the environmental variables (i.e., air temperature, wind speed, solar radiation, humidity, and cloud cover) needed to predict the crab temperatures. For all trials, weather conditions were typical of those found in the Bering Sea during the snow crab fishery. Seven thermocouples were inserted into each crab through small holes drilled through the shell to monitor temperatures in the center of the merus of all five legs, near the body center, and in the eye. Thermocouples were held in place by wrapping them around a plastic cable tie that was then secured around the distal portion of the merus of each leg (leg thermocouples) or around the medial portion of the merus of the chela and fourth walking leg (eye and body thermocouples). After the thermocouples were in place, crabs were placed in

cool seawater (3–8°C) and were allowed to equilibrate to the water temperature. At the beginning of a trial, crabs were removed from the seawater and placed on wire mesh to minimize conduction. Weather conditions near the crab were monitored throughout the trial. Air temperature was recorded along with crab temperatures by use of a thermocouple exposed to the air. Wind speed was measured with a cup anemometer (NRG Systems #40) positioned next to the crab. Total horizontal solar radiation was measured with a small pyranometer (Apogee Instruments) facing directly upward. Humidity was recorded with a data logger (Onset Computers model HO8-032-08). Measurements from all thermocouples, the anemometer, and the pyranometer were recorded at approximately 1-s intervals by a data acquisition device (Omega OMB-DAQ-56) connected to a laptop computer. Each trial lasted between 5 and 25 min.

A limited number of Tanner crabs were also tested between 8 and 9 December 2000 to determine the suitability of the snow crab model to this morphometrically very similar species. For these trials, crab temperatures were measured with thermisters placed in the center of the body and in the center of the merus of the second walking leg, and these temperatures were recorded at 1-s intervals with a small data logger (Onset Model HO8-008-04). Wind speed and solar radiation were measured with the same sensors described above, but measurements were recorded with a small data logger (Onset Model HO8-006-04) housed in a waterproof container. Every minute, relative humidity and air temperature were measured and recorded by a data logger (Onset Model HO8-032-08). Each trial lasted between 5 and 10 min, and data were downloaded to a computer after each trial.

After all trials were completed, the observed crab temperatures were compared with those predicted by the realistic and simple-shape models. For each second in the trial, the predicted crab temperature was subtracted from the measured value, and I calculated the root mean square (RMS) to yield a value that represented the average temperature difference between the observed and predicted crab temperatures. For these analyses, only the first 300 s of each trial were used so that only trials of the same duration were being compared. Also, 5 min (300 s) is about the average maximum time crabs are exposed to air during the fishery (Tracy and Byersdorfer 2000), so this period of each trial is the most relevant. For snow crabs, where temperature measurements and predictions were made for all legs and the crab body, a weight-

TABLE 2.—The average snow crab size and average February weather conditions in the Bering Sea, which were used for modeling simulations.

| Variable | Average value | Comments |
|---|---|---|
| Carapace width | 100 mm | Marketable size is 102 mm |
| Air temperature | −5°C | Average of the average daily minimum and maximum |
| Wind speed | 2 m/s | Average freestream wind speed (8 m/s) was reduced to approximate what the crabs actually experience |
| Relative humidity | 84% | |
| Percentage of sky clouded | 50% | |
| Total horizontal radiation | 50 W/m$^2$ | Approximate value at dawn and dusk |

ed average RMS for each trial was calculated to assess the performance of the model for the crab as a whole. The RMS for each leg was weighted by the calculated mass of that leg and its pair on the other side, and the body RMS was weighted by the mass of the body.

*Model simulations.*—The completed and tested model was then used to perform sensitivity analyses for various model inputs, including body size, $h_c$, and all weather parameters. Because the predicted cooling curves were very close to linear over the first 150 s, I calculated the cooling rate (°C/min) at 150 s and used this value as a comparative metric among the following simulations. For all simulations, average February values for St. Paul Island, Alaska, weather parameters and a crab size of 100 mm CW were used as default values (Table 2). A number of simulations were performed, varying one or two parameters within reasonable bounds.

To investigate the sensitivity of the model results to variation in the model parameters, I chose a parameter that had a large degree of uncertainty and that would probably have strong effects on the model results. The $h_c$ values were estimated from Nu–Re relationships that had coefficient of determination ($r^2$) values ranging from 0.62 to 0.84 for the legs and body and an $r^2$ value of 0.12 for the eye (Figure 1). In this model, $h_c$ governs both convective and evaporative heat transfer terms because the mass transfer coefficient is estimated from $h_c$. Combined, these two terms account for roughly half of the total heat budget of the crab. Thus, errors in estimating $h_c$ are likely, due to relatively low $r^2$ values, and any errors would be likely to produce large effects in the model results. To generate $h_c$ values that accounted for the observed variation in the Nu–Re relationships, I adjusted each relationship by the variation that was not explained by the regression (Figure 1). For example, the body Nu–Re relationship was Nu = 0.203Re$^{0.512}$ and the $r^2$ value was 0.68, so the upper and lower values of $h_c$ were generated by multi-

plying the right-hand side of the equation by 1.32 and 0.68. The first value was obtained by $1 + (1 − r^2)$. These upper and lower values of $h_c$, shown in Figure 1, were then used in the model to estimate cooling rates at various wind speeds; other weather variables reflected average Bering Sea conditions.

I also calculated cooling rates while varying body size, air temperature, wind speed, relative humidity, cloud cover, and solar radiation; all other variables were kept constant at the average Bering Sea conditions. To estimate the relative effects of each weather variable and body size, I converted the effect of each variable on cooling rate to an equivalent effect of air temperature change under average conditions, similar to calculating a wind chill value that gives the additional effect of wind on people in cold weather.

*Weather data.*—Weather data from St. Paul Island were used as inputs into the model. Data from 1979 through 2001 were obtained from the National Climatic Data Center and consisted of approximately hourly observations. The weather components used were wind speed, air temperature, humidity, cloud cover, and total horizontal solar radiation. Only data from 1979 through 1990 contained estimates of solar radiation. To generate estimates of solar radiation, I used data from 1960 to 1990 and correlated other weather components with solar radiation and then used these relationships to generate estimates of solar radiation from 1991 to 2001. Where data were missing, replacement data were generated by interpolating between known data points.

*Crab micrometeorology.*—To apply the thermal model in realistic situations, I needed to ascertain the weather conditions experienced by the crabs. The model requires weather inputs for air temperature, wind speed, humidity, solar radiation, water temperature, and cloud cover. I assumed that all of these except wind speed would not vary appreciably between the crab and a height of 10 m, where weather measurements are usually recorded. To assess the wind speed experienced by

crabs, I mounted an anemometer connected to a data logger in a crab pot. The pot was then lowered to the water surface and subsequently treated as if it contained crabs and was just hauled from the sea bed. The data logger recorded wind speed at 1-s intervals while a similar anemometer and data logger recorded wind speed on top of the wheelhouse of the vessel at the same rate. The two data loggers were synchronized so that simultaneous measurements of wind speed for a crab and the top of the wheelhouse could be compared. This procedure was repeated numerous times with the vessel in various likely orientations to the wind. The pot hauling gear was mounted on the starboard side of the vessel, and the wheelhouse was forward of the working deck. The vessel was oriented so that the wind came from one of four directions: (1) directly from port, (2) from the port side of the bow, (3) from the bow, and (4) from the starboard side of the bow.

To verify that the wind speeds felt by crabs recorded on the single vessel above were representative of crabs in the entire fishery, I used data obtained by required onboard observers. Observers monitored wind speed near the sorting table for a random selection of pot catches on all catcher–processor vessels and on a random sample of catcher-only vessels. Wind was measured with handheld anemometers, and observers were instructed to obtain measurements that were representative of winds experienced by crabs. In 2000, wind speed was recorded every 15 s for 90 s; in 2001, wind speed was an estimated average over a 20-s time period. For the 2000 data, the seven measurements were averaged to obtain each sampling datum. The date and time were also recorded during each sampling time. A total of 559 measurements were taken in 2000, and 783 measurements were taken in 2001. A total of 30 vessels were involved (21 in 2000; 25 in 2001), and these ranged in length from 23.8 to 54.9 m. The vessels covered a range of configurations; 10 vessels were catcher–processors and 20 were catcher-only. Nine of the vessels had the wheelhouse placed forward, 13 had the wheelhouse placed aft, and 8 had unknown wheelhouse placement. The configuration of some vessels was not known because the observers failed to supply the information.

Based on the St. Paul Island weather station data for 2000 and 2001, the wind speed closest in time to each onboard observation was extracted. Thus, onboard observations were matched to weather data from the same time. I assumed that the weather at St. Paul Island was similar to that occurring at the vessel during the observation. Most fishing is centered around St. Paul Island and occurs within about 100 km of the island. During periods when the weather is changing rapidly, the wind speeds at the vessel may be different than those at St. Paul Island at the same time, but otherwise I believe St. Paul Island wind speeds were representative of wind speeds near the vessel at the same time. The onboard observations were then regressed on the simultaneous St. Paul Island weather observations.

*Determination of critical cooling rates.*—I used the data by Warrenchuk and Shirley (2002b) to estimate critical cooling rates. They exposed snow crabs to cold air and wind in the laboratory for either 2.5 or 5 min and then monitored mortality and righting response. Using the conditions reported by these researchers, I calculated the cooling rates of the body and legs for average-sized crabs, large crabs (+1 SD), and small crabs (−1 SD), essentially replacing their wind chill values with a cooling rate (Figure 2). I then fitted logistic curves by eye for mortality of small crabs and righting response impairment of large crabs (Figure 2). I used small crabs for mortality because these generated curves that were the most resistant to rapid cooling rates, whereas the righting response impairment for large crabs generated curves that were the most susceptible to cooling, resulting in two curves spanning the entire range of responses to cooling. I fitted the logistic curves by eye because use of statistical techniques resulted in poor fits with the limited data. After I had generated logistic curves for both 5- and 2.5-min exposures based on the laboratory data, I generated a family of curves for exposure times of 1.0, 1.5, 2.0, 3.0, 3.5, 4.0, 4.5, and 5.5 min by assuming linear responses of crab mortality and righting response impairment to exposure time (Figure 2). The average sort time for crabs in the Bering Sea snow crab fishery is slightly less than 5 min from the initial exposure of crabs to air to the moment the last crab is returned to the sea (Tracy and Byersdorfer 2000), and I generated a logistic curve to predict the proportion of crabs returned to the sea over time (Figure 2). This exposure time curve was then combined with the mortality or righting response impairment curves generated for different exposure times to yield a single curve giving mortality or righting response impairment in terms of cooling rate of both the body and leg (Figure 2). In this manner, I accounted for the varying amount of time crabs are exposed to air in the fishery.

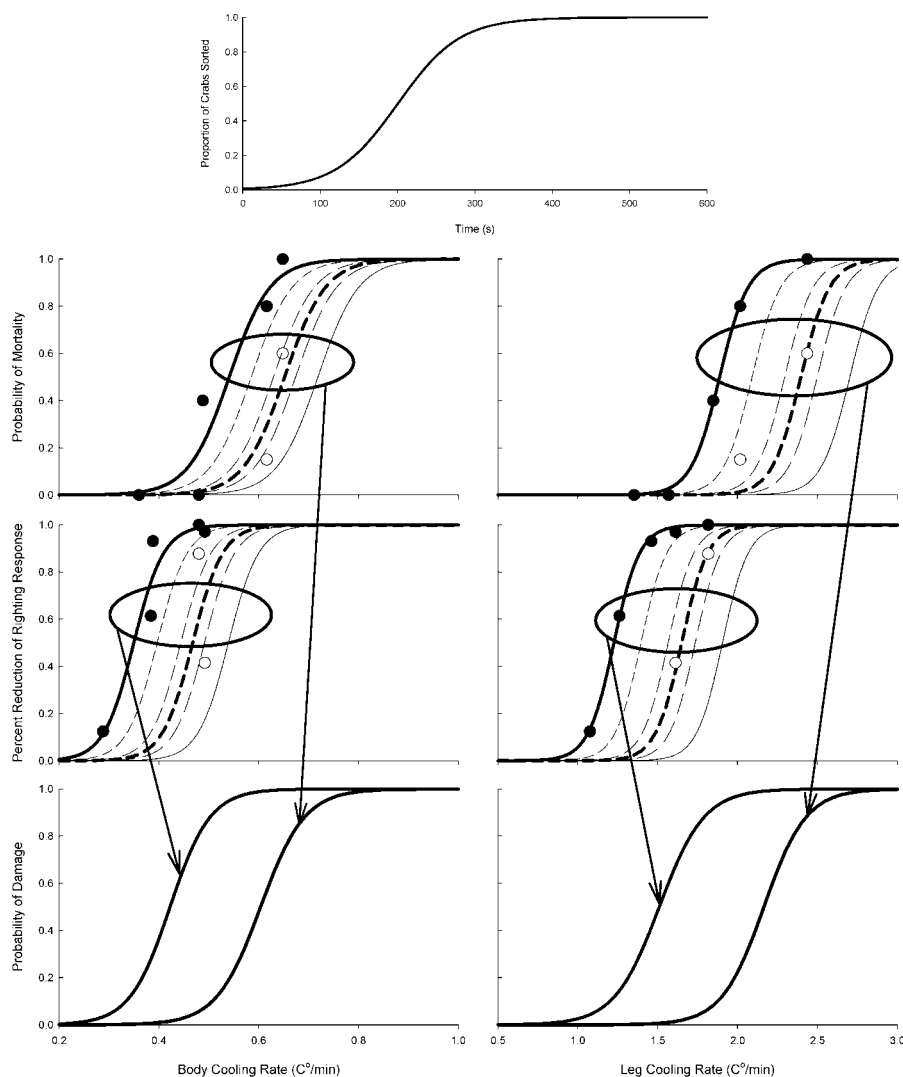*Management questions.*—Using the weather

FIGURE 2.—The steps involved in generating the critical damage curves for snow crabs. The top panel is the curve describing the exposure time of discarded crabs on the decks of vessels. In the next four panels, data from Warrenchuk and Shirley (2002b) are given by the closed (5-min exposures) and open circles (2.5-min exposures) after the cooling rates of their snow crabs were determined; logistic curves were fitted by eye to both the 5-min (solid black lines) and 2.5-min (dashed black lines) exposure data. Additional logistic curves were then generated (gray lines) for 1- (solid), 2- (long dash), 3- (medium dash), and 4-min (short dash) exposures. Additional curves for 1.5-, 3.5-, 4.5-, and 5.5-min exposures were also generated but are omitted from the graphs for clarity. The mortality and righting response graphs were generated from data for small and large crabs (see text for definition), respectively, based on both body (left panels) and leg (right panels) cooling rates. These logistic curves were then combined, indicated by the ovals on the graphs, with the exposure time curve to generate the critical damage curves (lower panels) that span the likely range of responses to various cooling rates (see text) and account for the various exposure times on deck.

data from St. Paul Island, I calculated a cooling rate for each hour of every season from 1979 through 2001 but only included those dates that fell between 15 January and 30 June. Cooling rates were calculated for a crab of 100 mm CW under the assumptions that the water temperature was 5°C, it took 45 s to get the crabs from the water to the sorting table or area, crabs were exposed to the sky with no covering structure, and catch was evenly distributed over the season.
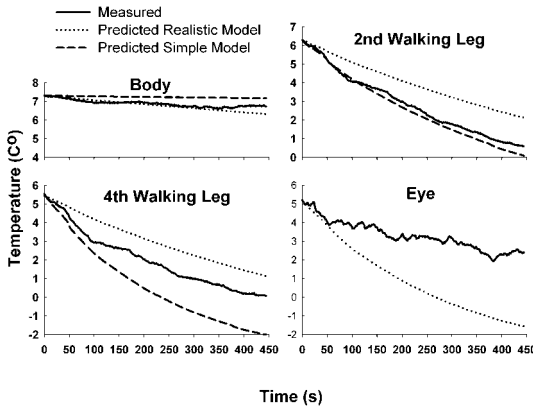
FIGURE 3.—Comparison of measured and predicted temperatures for one representative trial using both the realistic and simple-shape models.

To investigate the effect of changing the season starting date, I estimated the total probability of mortality for every hour during hypothetical 1-, 2-, 3-, 4-, and 6-week seasons from 1979 through 2001, starting on 15 January, 1 February, 15 February, 1 March, 15 March, and 1 April. I standardized the length of season rather than use the seasons as they actually occurred to eliminate any effect of season length on the results. For each season, I averaged the probability of damage over all hours to yield an estimate of damage due to cold-air exposure for each season.

When fishing hours were limited, the season length was extended so that about the same amount of crabs could be caught during the season. For these simulations, I assumed that the average soak time would be 24 h without any time restrictions and 48 h with limited fishing hours (Tracy and Byersdorfer 2000; van Tamelen 2001). On aver-

age, catch per pot is increased by about 28% by increasing the soak time from 24 to 48 h (van Tamelen 2001). Thus, with limited fishing hours, there would be fewer pot pulls but higher catch per pot, extending the season by 56%. I included three levels of limited fishing hours, all starting at 0800 hours and ending at 1800, 2000, or 2200 hours.

## Results

### Field Trials

The realistic model predicted crab body and leg temperatures fairly well; average RMS values were mostly less than 1°C (Figure 3; Table 3). Body error averaged 0.94°C, and most of the trials had predictions that were warmer than observed values (Table 3). The errors for the legs were generally less than the error for the body, averaging between 0.50°C and 1.03°C. The predictions for the chela (leg 1 in Table 3) and first walking leg (leg 2) were closest to observed values, and the accuracy of the model declined with successive legs. Also, observed temperatures fell below predicted temperatures more frequently as leg number increased; for the fourth walking leg (leg 5), all but one trial had observed temperatures that were less than predicted temperatures. The eyes were almost always (80%) warmer than predicted by the model, and they also had the largest error terms. For the few trials that were done with Tanner crabs, the model developed for snow crabs generally performed better than in the snow crab trials, as indicated by lower mean RMS values for both the body and the second walking leg (leg 3 in Table 3).

The simple-shape models performed similarly to the realistic models (Table 3; Figure 3). For the body and legs, the average RMS values for the

TABLE 3.—Root mean square temperature of snow crab and Tanner crab bodies, legs, and eyes based on the realistic and simple-shape models. Legs 1–5 refer to the chela and four walking legs. The weighted average (wt. avg.) is the average for the body and legs weighted by their mass.

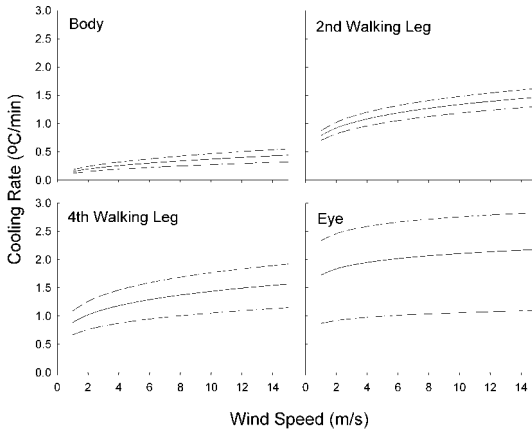| Model | Value | Body | Leg 1 | Leg 2 | Leg 3 | Leg 4 | Leg 5 | Eye | Wt. avg. |
|---|---|---|---|---|---|---|---|---|---|
| **Snow crab** | | | | | | | | | |
| Realistic | Mean | 0.94 | 0.52 | 0.50 | 0.72 | 0.82 | 1.03 | 1.38 | 0.76 |
| | SE | 0.18 | 0.06 | 0.07 | 0.10 | 0.16 | 0.18 | 0.19 | 0.14 |
| Simple shape | Mean | 1.20 | 0.98 | 1.63 | 1.29 | 1.32 | 1.36 | | 0.42 |
| | SE | 0.25 | 0.17 | 0.26 | 0.23 | 0.25 | 0.26 | | 0.10 |
| **Tanner crab** | | | | | | | | | |
| Realistic | Mean | 0.16 | | | 0.60 | | | | |
| | SE | 0.02 | | | 0.11 | | | | |
| Simple shape | Mean | 0.25 | | | 1.08 | | | | |
| | SE | 0.03 | | | 0.20 | | | | |

FIGURE 4.—The effect of varying the heat transfer coefficient within the range found in the Nusselt number–Reynolds number (Nu–Re) relationships (Figure 1) on the cooling rates of snow crab bodies, legs, and eyes at varying wind speeds. The solid line is from the best-fit Nu–Re relationship, and the upper and lower dashed lines were generated with the upper and lower Nu–Re relationships in Figure 1.

simple-shape models were always higher than for the realistic models. The bodies, or spheres, of the simple-shape model almost always predicted temperatures that were higher than measured temperatures, whereas the reverse was true for all but one of the legs, or cylinders. The weighted average RMS for the body and legs was less for the simple-shape model than for the realistic model, indicating that the simple-shape model performed better over the whole crab than the realistic model.

*Model Simulations*

The effects of variation in $h_c$ varied with crab part and wind speed (Figure 4). When $h_c$ was

changed to encompass the range of variation observed, the cooling rate of small body parts—the eye and fourth walking leg—deviated from average values by about 0.25°C/min and 1.0°C/min. In contrast, the cooling rates of the body and second walking leg varied from average values by about 0.03°C/min to 0.15°C/min, with similar variations in $h_c$. For low wind speeds (2 m/s), the variation due to uncertainty in $h_c$ was lowest for legs and highest for eyes (Table 4). The uncertainty in $h_c$ was similar to a change in air temperature of 1.0–1.2°C for the second walking leg (leg 3), 2.0–2.5°C for the body and the fourth walking leg (leg 5), and 3.7–5.1°C for the eye. Because the cooling rates of small body parts were greater than those of large body parts, the variation in cooling rates was also examined as a proportion of the mean cooling rate. The second walking leg had the least variation (about 10%), the body and fourth walking legs varied by about 25%, and the eye had variations up to about 50%. The range of variation also increased in all cases with wind speed; most of the increase occurred at lower wind speeds.

Larger crabs cooled more slowly than smaller crabs, and cooler temperatures resulted in more rapid cooling when all other parameters were held at average values (Figure 5). Smaller crab bodies cooled more rapidly than larger crabs in response to similar decreases in air temperature, and the same relationship held for the legs, indicating that smaller crabs were more sensitive to changes in temperature. The cooling rate for eyes, however, was relatively independent of crab size and varied mostly with air temperature. In terms of cooling rates, each 10-mm increase in CW was roughly equal to a 1°C increase in temperature (Table 4).

TABLE 4.—The relative importance of the heat transfer coefficient, body size, and various environmental conditions on the cooling rate of snow crabs compared with changes in air temperature. The equivalent change in air temperature (the change required to achieve a similar transfer of heat) is shown for the indicated change in each variable. Leg 3 refers to walking leg 2 and leg 5 to walking leg 4.

| Variable | Change in variable | Equivalent change in air temperature (°C) | | | |
|---|---|---|---|---|---|
| | | Body | Leg 3 | Leg 5 | Eye |
| Heat transfer coefficient (upper bound) | See Figure 1 | −2.29 | −1.22 | −2.47 | −3.69 |
| Heat transfer coefficient (lower bound) | See Figure 1 | 2.03 | 1.00 | 2.44 | 5.12 |
| Carapace width | 10 mm | 1.05 | 1.15 | 1.06 | 0.65 |
| Wind speed | 4 m/s[a] | −6.26 | −3.99 | −3.67 | −1.63 |
| Wind speed | 4 m/s[b] | −4.62 | −2.54 | −2.32 | −0.95 |
| Relative humidity | −80% | −3.09 | −3.28 | −3.11 | −3.48 |
| Percentage of sky clouded | −100% | −2.61 | −1.80 | −2.17 | −1.16 |
| Total horizontal radiation | 50 W/m2[c] | 1.23 | 0.91 | 1.17 | 0.62 |
| Total horizontal radiation | 300 W/m2[c] | 8.11 | 6.09 | 7.60 | 4.27 |

[a] From 1 to 5 m/s.
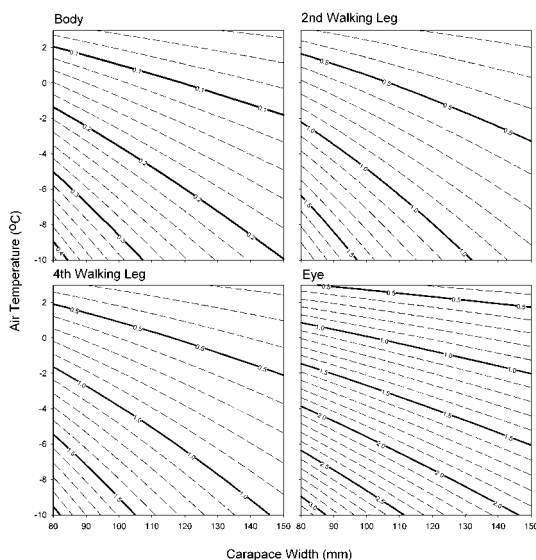[b] From 3 to 7 m/s.
[c] Starting at 0 W/m².

FIGURE 5.—The effect of snow crab body size and air temperature on the cooling rate (°C/min) of bodies, legs, and eyes. The cooling rate was calculated at 150 s; the starting temperature was 5°C.
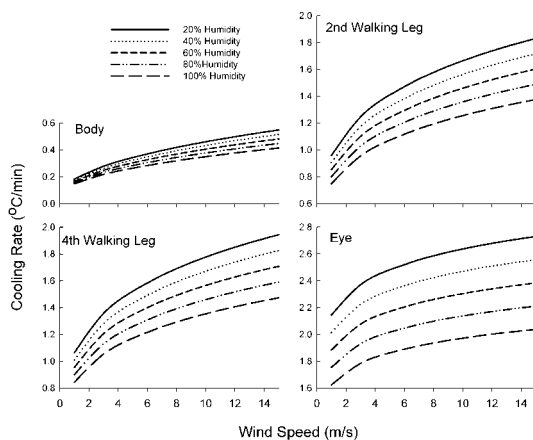


FIGURE 6.—The effect of wind speed and relative humidity on the cooling rate of snow crab bodies, legs, and eyes. The cooling rate was calculated at 150 s; the starting temperature was 5°C.

Higher wind speed and lower relative humidity resulted in more rapid cooling (Figure 6). The effect of humidity was small at low wind speeds but increased as wind speed increased. Humidity had a larger effect on legs and eyes than on the body. The effects of wind and humidity were synergistic: higher wind speed and lower humidity resulted in a proportionately greater cooling rate, especially for smaller crab parts. For a crab body with a 100-mm CW, an increase in wind speed from 1 to 5 m/s increased cooling rates similar to a decrease in air temperature of more than 6°C, but the equivalent decrease in air temperature was only about 4°C for legs and 1.6°C for the eye (Table 4). If wind speed increased from 3 to 7 m/s, the equivalent decreases in air temperature were 4.6, 2.5, and 1.0°C for the body, legs, and eye, respectively (Table 4). Decreases in humidity from 100% to 20% resulted in increased cooling rates similar to about a 3.25°C decrease in air temperature for all crab parts at a wind speed of 3 m/s (Table 4).

Decreased cloud cover and solar radiation resulted in more rapid cooling (Figure 7). For all crab parts, the effect of decreasing cloud cover was constant regardless of solar radiation levels. Even moderate solar radiation of 50 W/m², which is equivalent to twilight on a clear day in the Bering Sea, resulted in lower cooling rates; clear days resulted in even greater decreases in cooling rates. Decreases in cloud cover from 100% to clear skies resulted in increased cooling rates similar to a 2.6°C decrease in air temperature for the body, about a 2°C decrease for legs, and a 1.2°C decrease for the eye (Table 4). An increase in solar radiation from 0 to 300 W/m² resulted in decreased cooling rates similar to increases in air temperature of about 8°C for the body, 6.1–7.6°C for legs, and 4.3°C for the eye (Table 4).

*Micrometeorology Results*

The wind speed potentially experienced by crabs was always less than that measured on top of the wheelhouse (Figure 8). The average wind speed as a percentage of the wheelhouse wind speed varied
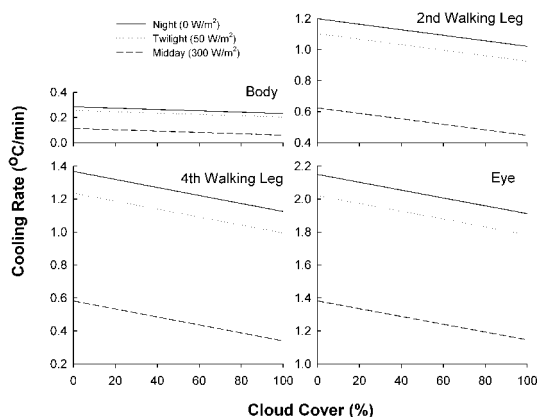


FIGURE 7.—The effect of cloud cover and solar radiation on the cooling rate of snow crab bodies, legs, and eyes. The cooling rate was calculated at 150 s; the starting temperature was 5°C.
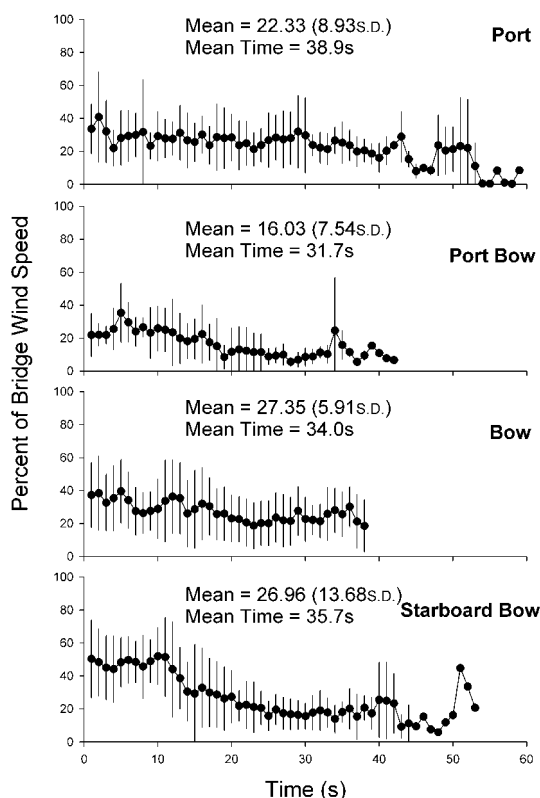
FIGURE 8.—The average ± SE wind speed measured in crab pots, expressed as a percentage of the simultaneous wind speed measured on top of the bridge, for various vessel orientations to the wind. The overall mean wind speed and the mean time required to retrieve the pot are given for each vessel orientation.
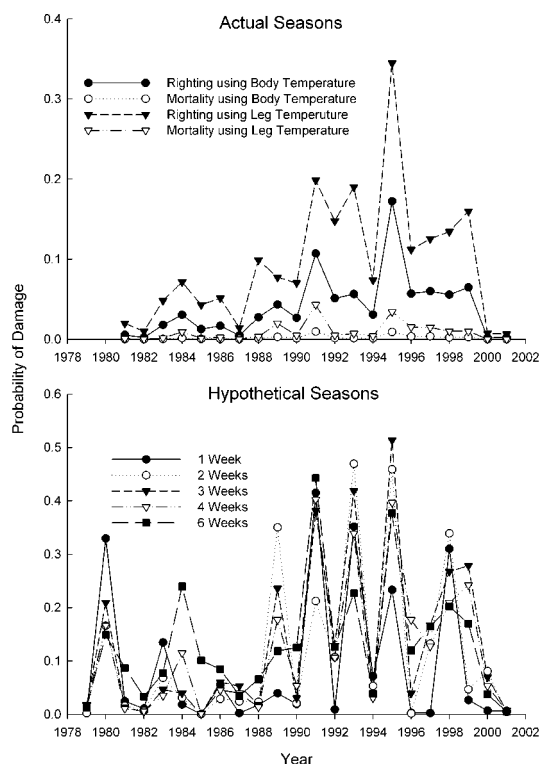


FIGURE 9.—Yearly variation in handling damage rates calculated based on actual and hypothetical seasons. Actual season values were calculated based on both righting response impairment and mortality as predicted by body and leg cooling rates. The hypothetical season values were calculated based on only the righting response impairment predicted by leg cooling rates, but they include data from seasons of various lengths.

from 16% to 27% during the pot hauling process, depending on vessel orientation to the wind. The average pot haul from water surface to deck was 30–40 s. Because the hauled pot was at the same level as and next to the sorting table, the wind speed at the end of the trial was probably representative of the wind speed experienced by crabs during the sorting procedure. For the remaining analyses, I assumed that the wind speed felt by crabs was equal to 25% of the measured wind speed.

The wind speed recorded on deck by observers generally increased with wind speed at St. Paul Island, but there was a large amount of variability; $r^2$ values were 0.081 and 0.056 for 2000 and 2001, respectively. The wind speed recorded at the crab sorting area was almost always a small fraction of the simultaneous wind speed at St. Paul Island, averaging 29% and 7.5% of the weather station wind speeds for 2000 and 2001. This result con-

firmed that the wind speed experienced by crabs during the fishery and on many different vessels is generally 25% or less of the wind speed measured at St. Paul Island.

*Variation in Years and Crab Responses*

When handling damage was estimated for the seasons as they actually occurred, seasons in the 1990s had higher damage rates than prior years (Figure 9). There was, however, a large amount of yearly variation; damage rates ranged from 0% to 30%. Use of righting response impairment and leg cooling rates resulted in higher damage rates than the use of mortality and body cooling rates. Because righting response predicted from leg cooling rates yielded the most sensitive measure of cold-air exposure, this variable was used for the remaining analyses. Similar patterns can be seen for all of the response variables except when values
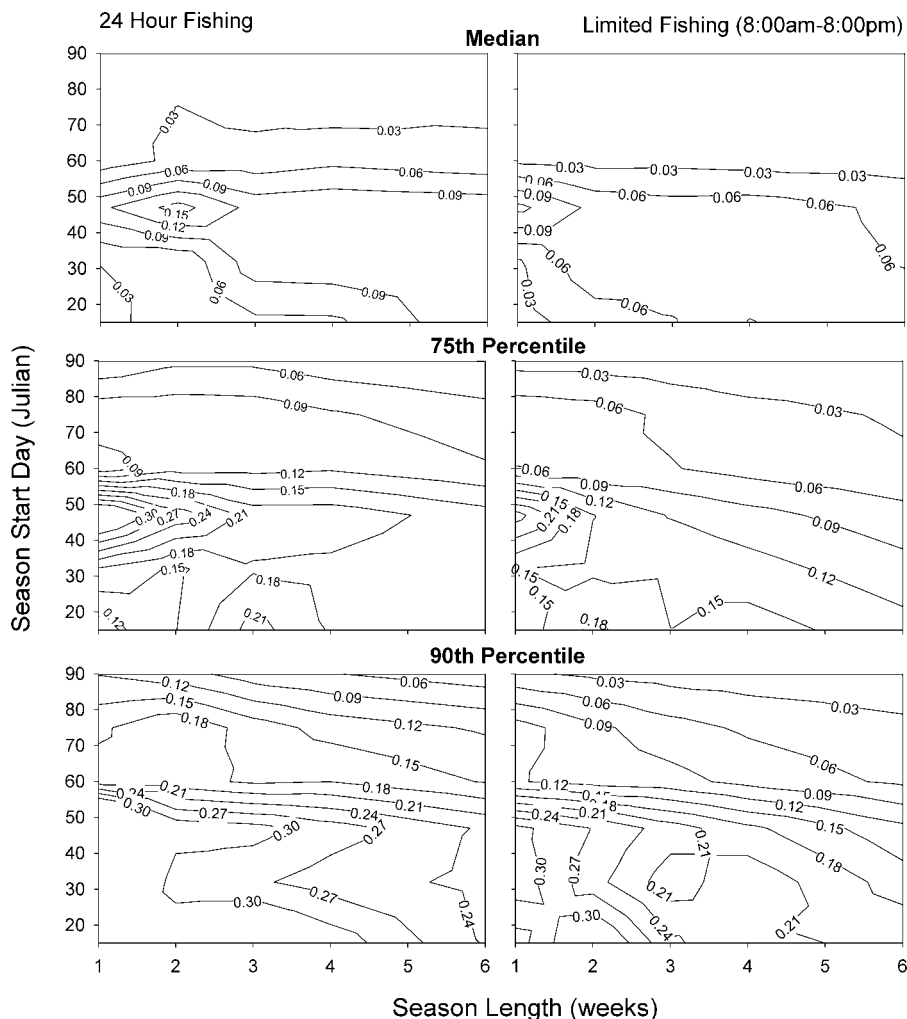
FIGURE 10.—Handling damage rates (contour lines), expressed as a percentage of snow crabs returned to the sea, for simulated seasons of varying lengths, start dates (days of the year), and fishing hours (24 h or limited to daytime). These graphs were generated based on the critical damage curve from the righting response impairment and leg cooling rate. The data were highly skewed towards low values, so the median, 75th percentile, and 90th percentile of all years are displayed. The percentiles indicate the percentage of seasons that fell at or below the given value.

are near zero. For all of the simulated season lengths, the estimated damage rate due to cold-air exposure varied from close to 0% to more than 40% during the 23 years investigated (Figure 9). Any variation in damage due to season length was trivial relative to the variation between seasons.

*Season Length, Start Day, and Limited Fishing Hours*

The data for these analyses were highly skewed. Most seasons had low damage rates, and a few seasons had much higher damage rates. For this

reason, parametric statistics were not usable, and the median, 75th percentile, and 90th percentile of all years were calculated and presented (Figure 10). Because righting response and leg cooling rates yielded the highest damage rates and the clearest results, they were used in this analysis. When other measures of damage were used, such as mortality and body cooling rates, the overall patterns were similar but the magnitude of the damage rates was lower. There was a slight tendency for longer seasons to have lower damage rates, but this effect was minor relative to the ef-

fects of season start day and limited fishing hours. Delaying the season start day from the current date of 15 January to 20 February (Julian day 15–50) only reduced damage rates for long seasons and limited fishing hours, whereas it increased damage rates for short fishing seasons and unlimited fishing hours. A start day of 1 March (Julian day 60) or later rarely resulted in damage rates of more than 10%. Limiting the fishing hours generally reduced the handling damage rate by 2–10% over all seasons and starting days. There was little difference among the three limited fishing hour options investigated.

## Discussion

The fate of bycatch and discards is poorly understood, and handling mortality may be an important and often ignored source of fishing mortality for a species. Understanding the mechanisms causing handling mortality over the range of possible fishing conditions is essential for estimating the magnitude of this form of fishing mortality (Davis 2002). Typically, estimates of handling mortality are generated by holding fish subjected to handling or simulated handling for short time periods or by use of tag and recapture methods (MacIntosh et al. 1996; Zhou and Shirley 1996; Olla et al. 1997; Davis and Olla 2001, 2002; Davis et al. 2001; DiNardo et al. 2002). Another approach is to correlate various factors with fish condition upon release under the assumption that fish condition is a good indicator of future mortality (Richards et al. 1995; Trumble et al. 2000). These methods, however, fail to identify the causal mechanisms of mortality. Thermal models have proven useful in other biological situations to predict activity schedules, distributions, and metabolic needs (Heath 1964; Porter et al. 1973; Mitchell 1976; Muth 1977, 1980; Porter and McClure 1984; Denny 1993; Bell 1995). If body temperature or the rate of change in body temperature is a good predictor of mortality, then handling mortality due to air exposure could be estimated. Based on thermal modeling, it was possible to reconstruct the entire thermal history of crabs caught during fisheries, given general weather conditions.

The model performed well given the complexity of the organism and the different body parts that were monitored. Cooling rates of the body and legs were predicted equally well, and predictions were best for the larger legs and worst for the eyes. Past models for marine organisms have predicted body temperature within a degree of measured values (Bell 1995; Helmuth 1998, 1999), which is slightly

better than the model presented here. The morphological complexity of crabs relative to the other tested organisms, mussels and seaweed, may account for the difference in performance. In contrast to the model here, these other models have been concerned with organisms getting too hot during low tides. If any section of the modeled crab part begins to freeze during the trial, some of the heat loss of the part will go towards freezing as the latent heat of crystallization, making the measured temperature greater than would be predicted by the model. This pattern of higher measured than predicted temperature was seen in about half of the legs modeled by the realistic crab model and almost all of the legs modeled by the simple-shape model. Hemolymph circulation can also affect the observed temperatures. If circulation is significant, the conduction of heat between the body and legs will be larger than expected. Most of the eye temperatures were higher than expected, and this is probably due to circulation between the eye and body.

Previous thermal modelers (e.g., Bell 1995; Helmuth 1998, 1999) have not documented the sensitivity of their models to variations in model parameters. The sensitivity of the crab model to variations in $h_c$ was less for larger parts than for smaller parts. Part of this effect was due to the larger variation observed in the Nu–Re relationships for the eyes and the last walking leg, but the thermal inertia of the part is probably more important. For example, the variation in the Nu–Re relationship for the body was relatively large, but the body also had fairly low sensitivity to variations in $h_c$. The sensitivity of the model to variations in $h_c$ suggests that this model is about equally affected by model specifics as by the input weather conditions. However, the general model specifications are the primary determinants of generalizations drawn from any model.

A modeling approach that substituted simple shapes for the crab body and legs produced a model that performed similarly to the more complex model based on real crabs. The simple-shape model, however, was less accurate and produced results that failed to capture some of the complexities identified by the realistic model. The simple-shape approach was much easier than the realistic model and required only information about the size and weight relationships of the crab body and legs rather than the Nu–Re relationships necessary for the realistic model. The idea of using simple shapes rather than realistic shapes is not new and has been shown to be useful in many situations (Mitchell

1976). A simple approach like this could be useful in situations where general thermal responses of marine organisms are needed. The more realistic model should be used when estimates of handling mortality will be generated for modeling and management purposes.

Modeling the heat budget for legs and other sensory appendages as well as the body may enhance our understanding of the long-term survival of crabs and the effect of sublethal exposure to cold air. Crabs often autotomize their legs when exposed to extreme cold (Carls and O'Clair 1990, 1995; Warrenchuk and Shirley 2002a, 2002b), and leg loss may lead to lower survival, growth, or reproductive output (Simonson and Hochberg 1986; Smith and Hines 1991; Smith 1995). Generally, the legs and eyes cooled more rapidly than the body, probably because of their lower mass and thermal inertia, indicating that these appendages may be more sensitive to cold-air exposure than the body is. Crabs that are experimentally exposed to cold air in the laboratory and then held in the laboratory may not exhibit any obvious signs of exposure; however, they may actually have lost function of their sensory appendages or legs, and their ability to locate food or avoid predators may be drastically reduced. Leg loss and righting response are more sensitive to cold-air exposure than mortality is (Warrenchuk and Shirley 2002a, 2002b), and both could be indicators of leg muscle or nerve damage. The smaller legs cooled more rapidly than the larger legs, and smaller legs are also more likely to be lost when crabs are exposed to cold air (Warrenchuk and Shirley 2002a, 2002b). Eyes cooled more rapidly than the legs, so these sensory organs may be even more sensitive to cold-air exposure than legs. Because of the increased sensitivity of appendages to cold-air exposure, the righting response as predicted by leg cooling temperature may be superior to laboratory mortality as an indicator of survival in the field.

Thermal modeling has demonstrated that factors affecting crab cooling rates are complex and often interrelated. Other than air temperature, the environmental factors that most affected the cooling rates of crabs were wind speed, humidity, solar radiation, and cloud cover. Of these, solar radiation had a large effect even at the modest level of 50 W/m², which occurs frequently in the Bering Sea. Wind speed is a driving force for both convection and evaporation, and variations in wind speed at the higher wind speeds common on vessel decks in the Bering Sea had less of an effect on crab cooling than did changes in wind speed under calmer conditions. The evaporative term, dependent upon both wind speed and humidity, became more important when humidity was low. In addition, cold air can hold less water vapor than warmer air, so the effect of humidity will be increased with colder air temperatures. Because the emissivity of clear skies (~0.68) is substantially lower than that of cloudy skies (~0.95), crabs cooled faster under clear skies due to radiative exchange with the sky. Based upon these results, crab cooling rates are likely to be most rapid on cold, clear, breezy nights. Under these conditions, radiation of heat to the sky is maximized due to low sky emissivity, solar heating is eliminated, and humidity is likely to be low. Although wind chill, a simple measure of weather severity, may be attractive due to its ease of use (Warrenchuk and Shirley 2002a), this metric ignores the potentially large effects of humidity, solar radiation, and cloud cover. High values of solar radiation can easily overcome the effects of increased wind speed, as can the combined effects of cloud cover and humidity. For these reasons among others, wind chill is a poor substitute for total heat budgets (Bluestein 1998; Bluestein and Zecher 1999).

This study has identified some environmental factors that may contribute to the handling mortality of crabs exposed to air during cold-weather fisheries. Numerous studies have identified air temperature or "environmental" factors as potential causative agents of handling mortality (Powles 1969; Brown and Caputi 1983; Richards et al. 1995). Additional studies have exposed individuals to various temperature regimes, either colder or warmer than normal (Carls and O'Clair 1990, 1995; Olla et al. 1998; Davis and Olla 2001, 2002; Davis et al. 2001; DiNardo et al. 2002), and these have shown that temperature is important in determining the rate of handling mortality. However, all of these studies suffer from a lack of understanding of the dynamics of heat exchange and the way various factors can affect body temperature. The additional effect of wind can be clearly seen by comparing crabs held in still, cold air and those held in windy conditions. About 50% of the crabs held at −8°C for 32 min in still air died (Carls and O'Clair 1995), but it only took a 5-min exposure to kill about 50% of the crabs at slightly warmer temperature (−6°C) in the presence of an 8-m/s wind (Warrenchuk and Shirley 2002b). All of these studies ignore the additional and nontrivial effects of radiative heat exchange, solar radiation, and evaporation, which were shown to be important here. Evaluation of all factors, not just air tem-

perature and wind speed, is necessary to understand how handling mortality is affected by environmental conditions.

The amount of seasonal variation was large for hypothetical seasons as well as for actual seasons. Damage rates ranged from near 0% to about 50% for the most sensitive measure of damage. The severity of a season was dependent upon a period of severe weather occurring simultaneously with the season. Severe weather conditions are likely in January and February but can also occur in March and April. Shorter seasons can be severe if they coincide with severe weather, but they may also miss severe weather entirely. Long seasons, on the other hand, are likely to encompass at least some severe weather, but a higher proportion of the long season occurs at times when severe weather is unlikely (i.e., March or later), resulting in lower overall damage rates than are observed for shorter seasons. This probably explains the general increase in damage rates over time observed for the actual seasons. In the 1990s, the seasons were about 3–10 weeks in length; therefore, they were likely to encounter some severe weather but had little time to encompass more benign weather conditions. In contrast, the seasons in the 1980s were very long and extended into the summer in many cases. The 2000 season was delayed until 1 April due to sea ice on the fishing grounds, and the 2001 season was very short and missed severe weather events by chance. It is clear that the handling damage due to cold-air exposure is not constant and can vary dramatically.

From the perspective of a fishery manager, there are at least two methods that could be implemented to reduce crab handling damage due to cold-air exposure. First, the fishing season could be conducted at a time of year when the weather conditions are not as severe for crabs. Based on the model developed here and past weather data, a season start date of March 1 or later would be needed to achieve any appreciable reduction in handling damage. Even with these later start dates, there will be some years that produce damage rates of 15% or more (especially with shorter seasons), but this will occur in less than 10% of the years (Figure 10, 90th percentile). If the starting date, however, is shifted from the current date of 15 January to sometime in February, handling damage rates may be increased slightly rather than decreased. The second option open to managers is to limit the hours in which fishing can occur. Limiting fishing to daylight hours may reduce damage rates substantially. If fishing hours are limited in

combination with delaying the season start date to March or later, handling damage rates will be reduced to 6% or less for almost all years. From this analysis, the average and percentile changes in handling damage can be estimated for both management actions independently and in concert.

There are some actions fishers can take to reduce handling effects due to cold-air exposure. Many sorting tables are made of aluminum, and such tables have two potential effects on the heat budget of crabs. First, aluminum is a very good conductor of heat, and any crabs in contact with the table will lose heat rapidly through conduction. Second, the emissivity of aluminum is low, ranging from 0.04 to 0.4. Aluminum sorting tables will therefore act as heat sinks for long-wave radiation. The emissivity of weathered aluminum sorting tables is similar to that of extremely clear skies, so a crab suspended above an aluminum sorting table can actually cool to a temperature below the ambient temperature. A simple method to eliminate these properties of aluminum sorting tables is to cover the table with a different material that has low heat conductance and a high emissivity, such as wood or plastic. Covering sorting areas with roofs or other structures will also reduce heat loss via long-wave radiation to the sky when the sky is clear or partially clear, as long as the covering is not made of exposed aluminum.

Although this model was developed for a high-latitude winter fishery, there is no reason why a similar approach cannot be applied to fisheries in warm regions where organisms may be exposed to severe heating. For example, lobsters (*Panulirus marginatus* and *Scyllarides squammosus*) caught in the northwestern Hawaiian Islands can be subjected to bright sun and warm air temperatures for hours before being returned to the sea (DiNardo et al. 2002). These lobsters go from relatively constant thermal conditions in cool water, pass through a thermocline where they heat rapidly to ambient water temperature, and are subjected to hot air conditions while they are sorted; upon release, they must cool rapidly to surface water temperature and then cool further to their normal temperature range. Most of the change in temperature while transitioning from water to air is rapid and takes place in a matter of minutes, and lobsters may reach temperatures of 10°C or more above their thermal normal. This mechanistic approach to assessing handling mortality could also be used in other fisheries where discard mortality is a concern. Many fisheries catch nontarget species, and the survival of these species may depend at least

in part upon the thermal regime experienced during capture. Understanding and assessing the mechanisms that cause handling mortality, rather than using simplistic surrogates such as air temperature and wind speed, will lead managers to make informed and effective decisions to reduce this source of mortality. Although developed with a specific fishery in mind, the modeling approach taken here potentially has wide application to many fisheries around the world.

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